

REPRODUCTIVE ATTRIBUTES OF SOME ROCKY MOUNTAIN SUBALPINE HERBS IN SUCCESSIONAL CONTEXT

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ABSTRACT.— Selected reproductive attributes of herbaceous plant species were compared among three stages of a sere in the subalpine zone of Utah's Wasatch Mountains: herbaceous meadow, aspen grove, spruce-fir forest. No successional trends in seed size or inferred mode of seed dispersal were detected. We ascribe the deviation of these findings from those of most other studies to differences in climate, life-form composition, or community age between our sere and those of other studies. A variety of flower colors were found in the meadow stage, grading into a predominance of white flowers under conifers. Animal vectors of pollen, capable of effecting plant outcrossing, were most abundant in the meadows and an order of magnitude less abundant under aspen.

Attempts to develop inductive generalizations about ecological succession have included studies of reproductive characteristics of plants. Among the earliest were those of Salisbury (1942), who found British woodland species to have heavier seeds than those of species in open vegetation. This was largely due to woody species having heavier seeds than herbs, but forest herbs were also heavier seeded than meadow herbs. Salisbury suggested that low light intensity on forest floors favored individuals with stored materials in the seed sufficient to fabricate a greater light-intercepting surface. These results have been generally corroborated for grassland (Hayashi 1976, Werner and Platt 1976) as well as forest (Opler et al. 1977, Abrahamson 1979) seres. The statistical significance of these increases in seed size during succession has not been established. Marino (1980) found no significant difference in seed size of foredune herbs and shrubs from those under dune forest, but those of the intermediate slack dune stage were significantly smaller.

The mode of seed dispersal, as inferred from diaspore morphology, has been suggested to change toward a greater frequency of animal dispersal as forest succession proceeds (Dansereau 1957, Dansereau and Lems 1957, Harper et al. 1970, Johnston and Odum 1956, Pijl 1972, Opler et al. 1977). Hayashi

(1976) did not detect this trend in a grassland sere. Several of these authors, as well as others, suggest that animal dispersal adaptations may be more common among woody species than among herbaceous species. If so, the successional changes in dispersal mode may be due to changes in the proportions of various life forms. Statistical tests of these trends are lacking.

Most of the above studies were conducted in temperate deciduous forest or tropical moist forest biomes. Our study examined some plant reproductive attributes in stands along a sere terminating in subalpine coniferous evergreen forest. Seed sizes, dispersal modes, flower color frequencies, and abundance of animal pollen vectors most likely to effect floral outcrossing were compared among the stages of this sere.

STUDY AREA AND METHODS

Field work was conducted in the subalpine zone of the Wasatch Mountains in extreme northern Utah. The presumed sere involves vegetative colonization of well-drained, herb-dominated meadows by clones of quaking aspen, *Populus tremuloides* Michx. The climax forest is dominated by subalpine fir, *Abies lasiocarpa* (Hook.) Nutt., and Engelmann spruce, *Picea engelmannii* Parry. No other

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woody species are significant community components. For further discussion of community dynamics and a site description, see Schimpf et al. (1980).

For each stage of succession, we selected abundant herbaceous species producing substantial numbers of seed, thus excluding vegetative remnants of earlier stages. Species were included if they produced at least 100 seeds from a total of 10 or more mother plants within a 0.2-ha rectangular plot during the summers of 1976, 1977, or 1978. There was one such plot for each stage in the example of the sere known as Big Meadow (Schimpf et al. 1980): meadow, aspen, fir, spruce-fir. The species inclusion criteria proved unworkable for the fir and spruce-fir plots, owing to lower population densities and seed production per plant; these plots were treated as a single 0.4-ha conifer plot to determine species inclusion and for all data analyses. Species which qualified for inclusion were all counted equally in the analyses of reproductive attributes, rather than being weighted by abundance.

Total weight was determined for a sample of 100 seeds (or caryopses or achenes) for each species in a stage. Samples had been heated overnight at 100 C after collection to stop respiration. All seeds and caryopses were inspected microscopically, and all achenes sectioned transversely to confirm seed development before being weighed to the nearest 0.1 mg, in equilibrium with atmospheric humidity. Size was expressed as mean mg per seed. Baker (1972) reported that mean seed sizes of a group of plant species are often not normally distributed. The distribution of mean sizes in each stage was tested for normality with the Kolmogorov-Smirnov method (Sokal and Rohlf 1969), using both untransformed and log-transformed variates. Transformed mean seed sizes were compared among stages by analysis of variance. Pairs of stages were compared for their intrinsic variation in mean sizes by the F-ratio of variances (log-transformed data) (Lewontin 1966).

Flower color was recorded in the field for each species. The presumed mode of dispersal was classified as animal, wind, or other from inspection of diaspore structure. The frequency distributions of flower color and dispersal mode categories were compared

among stages by chi-square tests. Chi-square was also employed to test for differences in frequency of animal dispersal modes among different plant life forms.

Insects suspected to be capable of effecting floral outcrossing were sorted from the general collections of insects associated with the herbaceous layer. Suspected pollinators included all adults in the following families: Syrphidae, Bombyliidae, Colletidae, Halictidae, Andrenidae, Megachilidae, Apidae, Sphingidae, Nymphalidae, Lycaenidae. These collections were obtained by D-Vac sampling of from 130 to 310 randomly chosen 0.50-m² or 0.25-m² plots that had been quickly covered with an insect-tight cage (Southwood 1978). Samples were taken at regular intervals throughout the 1977 and 1978 growing seasons in nearby examples of the successional stages similar to those at Big Meadow. Results were expressed as m² sampled per pollinator caught.

RESULTS

The 46 herbaceous taxa studied included 26 species in the meadow plot, 22 taxa in the aspen plot (including two varieties of one species), and 23 species in the conifer plot (Table 1). Mean seed sizes fail to exhibit a normal distribution within a stage, based on the Kolmogorov-Smirnov test. Following log transformation, all three stages show a normal distribution. The mean and standard deviation of transformed variates is depicted for each stage in Figure 1. None of the F values are significant at the .05 level; the means and variances of seed sizes in the three stages are statistically indistinguishable. No successional trends in community seed size are apparent. There are also no discernible patterns of size change within the set of those species that occupy two or more stages (Table 1), based on sign tests (Sokal and Rohlf 1969). White-flowered species become increasingly frequent and the red- and blue-flowered species less frequent through successional time, although this trend was not significant at the 0.05 level (Table 2). Modes of dispersal have similar frequencies in all three successional stages (Table 3), suggesting that there is no trend in this attribute.

Pollen vector abundance was notably lower during 1977 than during 1978 (Table 4). In both summers, abundance is an order of magnitude greater in the meadows than in

the aspen understory, with intermediate values in conifer understory. The most abundant pollinator families in the meadows were Halictidae, Apidae, and Syrphidae, each about

TABLE 1. Reproductive attributes of the herbaceous taxa.

Taxon	Mean seed size, mg			Flower color	Dispersal mode
	Meadow	Aspen	Conifer		
<i>Achillea millefolium</i> L. ssp. <i>lanulosa</i> (Nutt.) Piper	0.166	0.157	0.197	White	Other
<i>Agoseris aurantiaca</i> (Hook.) Greene var. <i>aurantiaca</i>	3.017	2.513		Orange	Wind
<i>Agropyron trachycaulum</i> (Link) Malte var. <i>glaucum</i> (Pease & Moore) Malte		3.359	3.324	Green	Animal
<i>Agropyron trachycaulum</i> (Link) Malte var. <i>latiglume</i> (Scribn. & Smith) A. A. Beetle	2.807	3.125		Green	Other
<i>Androsace filiformis</i> Retz.			0.359	White	Other
<i>Aquilegia coerulea</i> James var. <i>ochroleuca</i> Hook.			1.318	White	Other
<i>Arabis drummondii</i> Gray	0.255			Pink	Wind
<i>Arnica cordifolia</i> Hook. var. <i>cordifolia</i>			1.080	Yellow	Wind
<i>Arnica parryi</i> Gray			1.462	Yellow	Wind
<i>Aster engelmannii</i> (Eat.) Gray			3.091	White	Wind
<i>Aster integrifolius</i> Nutt.	1.932			Blue	Wind
<i>Bromus carinatus</i> Hook. & Arn.	6.905			Green	Animal
<i>Castilleja miniata</i> Dougl. var. <i>miniata</i>		0.383		Red	Wind
<i>Claytonia lanceolata</i> Pursh var. <i>lanceolata</i>	0.740	0.823	0.782	White	Other
<i>Collomia linearis</i> Nutt.	2.141			Pink	Other
<i>Delphinium nuttallianum</i> Pritz. var. <i>nuttallianum</i>	0.601			Purple	Other
<i>Descurainia richardsonii</i> (Sweet) Schulz var. <i>sonnei</i> (Robins.) C.L. Hitchc.		0.206	0.205	Yellow	Other
<i>Draba stenoloba</i> Ledeb. var. <i>nana</i> (Schulz) C.L. Hitchc.			0.084	Yellow	Other
<i>Epilobium brachycarpum</i> Presl	0.115		0.125	White	Wind
<i>Epilobium lactiflorum</i> Haussln.	0.802			Pink	Wind
<i>Erigeron speciosus</i> (Lindl.) D.C. var. <i>macranthus</i> (Nutt.) Cronq.		0.263	0.294	Blue	Wind
<i>Eriogonum heracleoides</i> Nutt.	2.786			Yellow	Other
<i>Erysimum asperum</i> (Nutt.) D.C. var. <i>purshii</i> Durand		0.719		Yellow	Other
<i>Erythronium grandiflorum</i> Pursh	5.125	5.992	6.660	Yellow	Other
<i>Galium bifolium</i> Wats.	2.427	3.260	3.338	White	Animal
<i>Geranium viscosissimum</i> Fisch. & C.A. Meyer var. <i>nervosum</i> C.L. Hitchc.	11.065			Pink	Other
<i>Gilia aggregata</i> (Pursh) Spreng.	1.369			Red	Other
<i>Hackelia micrantha</i> (Eastw.) J.L. Gentry	3.621	4.058		Blue	Animal
<i>Hieracium albiflorum</i> Hook.			0.430	White	Wind
<i>Hieracium scouleri</i> Hook.	0.814	0.926		Yellow	Wind
<i>Hydrophyllum capitatum</i> Dougl. var. <i>capitatum</i>			4.752	White	Other
<i>Ligusticum filicinum</i> Wats.		6.501	5.932	White	Other
<i>Lupinus argenteus</i> Pursh var. <i>rubricaulis</i> (Greene) Welsh	27.706	26.478		Blue	Other
<i>Madia glomerata</i> Hook.	2.664			Yellow	Other
<i>Osmorhiza chilensis</i> Hook. & Arn.		7.746	4.673	White	Animal
<i>Osmorhiza occidentalis</i> (Nutt.) Torr.	12.666	13.953		White	Other
<i>Pedicularis racemosa</i> Dougl. var. <i>alba</i> (Pennell) Cronq.			1.976	White	Other
<i>Poa nervosa</i> (Hook.) Vasey var. <i>wheeleri</i> (Vasey) C.L. Hitchc.		0.470	0.580	Green	Other
<i>Polygonum douglasii</i> Green var. <i>douglasii</i>	2.039			White	Other
<i>Potentilla arguta</i> Pursh var. <i>convallaria</i> (Rydb.) Th. Wolf	0.276			Yellow	Other
<i>Rudbeckia occidentalis</i> Nutt. var. <i>occidentalis</i>	2.070	1.657		Yellow	Other
<i>Senecio crassulus</i> Gray		2.633	2.855	Yellow	Wind
<i>Senecio serra</i> Hook.	0.745			Yellow	Wind
<i>Stipa lettermanii</i> Vasey	1.105			Green	Animal
<i>Trisetum spicatum</i> (L.) Richter		0.165	0.172	Green	Animal
<i>Viola nuttallii</i> Pursh var. <i>major</i> Hook.		3.944	3.478	Yellow	Animal

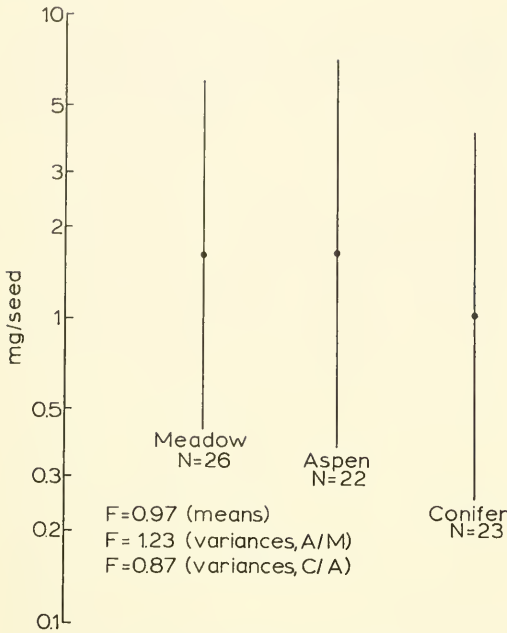


Fig. 1. Seed sizes of species in each stage of succession, depicted on log-scale. Dots represent means of log-transformed species means for each stage, with bars extending one standard deviation above and below these. N is the number of species in a stage. None of the F values are statistically significant.

12–15 m² per individual averaged over the two years. So few pollinators were caught in the forest understories that we cannot recognize their numerically dominant families with confidence.

DISCUSSION

Several explanations can be offered for the lack of a successional increase in seed size (Fig. 1). Unlike almost all seres for which seed size has been studied, ours does not include a pioneer stage. The meadows we studied have apparently been unforested for cen-

turies and are being slowly invaded vegetatively by forests due to climatic change (Schimpf et al. 1980). Thus, we do not expect the meadows to be dominated by species with light, highly vagile diaspores to the extent that recently deforested sites often are.

Likewise, our study site differs considerably from the deciduous forest and tropical moist forest sites of other studies with respect to environmental conditions. Soil at our site dries quickly after snowmelt, and summer rain is far less than potential evaporation. This is especially marked in the meadows, where evaporative potential is more than twice that under the conifer canopy (Schimpf et al. 1980). Because low moisture availability has been correlated with greater seed size, both interspecifically (Baker 1972) and intraspecifically (Schimpf 1977), the dryness of the meadows may offset the dim illumination of the spruce-fir understory as a force selecting for larger seeds. Marion (1980) found equally large seeds in the most xeric and most shaded stages of a sere.

Some reports of increases in seed size with succession appear to be equivocal. Werner and Platt (1976) found greater seed sizes of herbaceous *Solidago* species in climax than in seral ecosystems, but this is confounded by the location of the climax stand in a drier climate than that of the seral stand. The significance of an interspecific successional increase in herb seed size (Abrahamson 1979) is due to the presence of a single large-seeded climax species; no significant increase can be shown if the sizes are first normalized by log transformation. Perhaps the most noteworthy seed size increases during succession are those associated with shifts in life form composition.

A number of recent community-level studies of flower color in western North America concur that white flowers are relatively more

TABLE 2. Number of species in each flower color category in each successional stage.

Color category	Meadow	Aspen	Conifer
Red, orange, or pink	6	2	0
Blue or purple	4	3	1
Yellow	7	7	7
White	6	6	12

$\chi^2 = 10.70, .05 < P < .10$

TABLE 3. Number of species in each dispersal mode category in each successional stage.

Type of dispersal	Meadow	Aspen	Conifer
Animal	4	6	5
Wind	7	5	7
Other	15	11	11

$\chi^2 = 1.46, P > .25$

TABLE 4. Abundance of pollinators capable of effecting floral outcrossing. Total area D-Vac sampled over the course of the summer and area sampled per pollinator caught is expressed for each successional stage.

Year	Meadow		Aspen		Conifer	
	m ² sampled	m ² per pollinator	m ² sampled	m ² per pollinator	m ² sampled	m ² per pollinator
1977	155	5	59	59	33.5	8
1978	97	2	36.5	19	32.5	6

frequent under dense forest canopies than in better illuminated layers of vegetation (Baker and Hurd 1968, Daubenmire 1975, Moldenke 1976, Ostler and Harper 1978, del Moral and Standley 1979), but do not take a successional perspective. The similar pattern in our stands (Table 2) leads us to believe that a shift toward white-flowered species may be a widespread successional trend, but this also needs to be tested with seres including pioneer stages. We resist the temptation to propose functional interpretations of this pattern on the basis of human visual perceptions, which differ from those of pollen vectors, especially in the ultraviolet region (Kevan 1978, Goldsmith 1980). A spruce canopy acts as a neutral filter in the visible range, even when sun flecks are not considered (Federer and Tanner 1966). Therefore, the potential visibility of various colors (on a relative scale) probably changes minimally along our sere. Though we might expect the conifer understory to be bathed in radiation somewhat enriched in ultraviolet relative to visible (Vézina and Boulter 1966), white flowers may be the least UV-reflective (Guldberg and Atsatt 1975); thus the importance of signals in the ultraviolet may not change much during succession.

The similar frequencies of dispersal modes in all stages (Table 3) perhaps simply reflects the lack of change in life form composition in the lower strata of the sere. Shrubs and woody vines, surmised to have high proportions of species possessing adaptation for animal dispersal, are commonly thought to be most important in intermediate stages of seres, though we are not aware of any rigorous tests of this hypothesis. It is interesting that Thompson and Willson (1978) demonstrated more rapid vertebrate removal of fleshy fruits when experimentally provided at a forest edge than when placed beneath a closed forest canopy, implying that temper-

ate frugivores frequent intermediate seral stages, perhaps in response to vegetation physiognomy.

The differences among successional stages in abundance of pollinators reported in Table 4 are large, but nonetheless underestimated. Several strong-flying vectors were not sampled by the D-Vac technique, but were common to abundant nectar feeders in meadows. These were the sphinx moth *Hyles lineata* (Fabricius) and the hummingbirds *Selasphorus platycercus* (Swainson) and *S. rufus* (Gmelin), which visited primarily *Gilia*, *Delphinium*, and *Geranium* flowers. We casually observed essentially no moth activity in the forests, but expect some associated with the bloom of *Aquilegia* there. Smith (1982) quantitatively recorded hummingbird feeding in aspen understory but only transient flights through spruce-fir stands.

The level of herbaceous productivity undoubtedly affects the abundance of associated vectors. Lower pollinator densities in 1977 (Table 4) are associated with reduced herb aboveground productivity following an exceptionally dry winter (Schimpf et al. 1980). Within years, differences among stages in vector abundance do not correlate well with differences in herbaceous aboveground phytomass; meadow standing crop is four times that of herbs under conifers, and two to three times that of aspen understory (Reese 1981). Vectors respond, of course, to pollen and nectar rather than to total primary production, but we lack the requisite data to evaluate floral resource levels. The apparent low density of pollinators in aspen understory awaits elucidation.

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